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# How does photosystem 2 split water? The structural basis of efficient energy conversion

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Photosystem 2 (PS2) is the part of the photosynthetic apparatus that uses light energy to split water releasing oxygen, protons and electrons. Here, we present a model of the subunit organization of PS2 and the accompanying secondary antenna systems (phycobilisomes in cyanobacteria and the light-harvesting complexes in higher plants) and discuss possible physiological consequences of the proposed dimeric structure of PS2.

**PHOTOSYSTEMS CATALYSE THE** conversion of light energy, captured by chlorophyll, into forms that can be used by cyanobacteria, algae and higher plants. Within this process, photosystem 2 (PS2) is responsible for splitting water to form molecular oxygen, electrons and protons[1], a process assisted by photosystem 1 (PS1) and the cytochrome $b_6f$ complex. These events are vital for maintaining the present levels of biomass on our planet and for sustaining an oxygenic atmosphere.

Despite its importance, the reaction centre within PS2 that splits water is not fully understood at a molecular level. Most of our present knowledge on the structure–function relationship of this photosystem is drawn from analogies with reaction centres of photosynthetic purple bacteria (see Fig. 1), for which a high resolution three-dimensional structure is available[2]. Although useful, this comparison is restricted, as phototrophic purple bacteria do not split water and their subunit composition is much simpler than that for PS2. In PS2, the chlorophyll-binding proteins CP43 (PsbC*) and CP47 (PsbB) harvest light and transfer energy to a special form of chlorophyll *a*, P680, which is bound within a reaction centre composed of the D1 (PsbA) and D2 (PsbD) proteins; closely associated with this are the cyt $b_{559}$-binding subunits (PsbE/F) and the extrinsic 33 kDa subunit (PsbO). The latter is believed to shield a water-splitting manganese complex on the lumenal side (see Fig. 2). In addition, the chlorophyll *a*-binding and the chlorophyll *b*-binding proteins in higher plants and green algae, or the phycobiliproteins in cyanobacteria and red algae form additional and extensive light-harvesting systems for PS2.

Although cross-linking experiments and studies with both site-directed and deletion mutants of cyanobacteria have given clues as to how all these subunits are arranged[3,4], recent data obtained by electron microscopy has given further clues as to how these various light-harvesting and other systems are arranged relative to the D1 and D2 proteins.

## The PS2 core complex: the smallest unit that can split water

**The PS2 monomer.** Monomers of a PS2 core complex isolated from cyanobacteria, green algae and higher plants have a molecular mass of about 250–300 kDa, which is consistent with the presence of each of the major subunits in one copy (i.e. D1, D2, cyt $b_{559}$, CP43, CP47 and the extrinsic 33 kDa subunit) and about 40 chlorophyll molecules per monomer[5]. Transmission electron micrographs from cyanobacteria show elliptical particles with dimensions of 7.5 · 12 nm (Ref. 6), while identical monomeric particles, reconstituted into liposomes, showed individual spherical–ellipsoidal 10–13 nm particles in freeze-fracture electron micrographs[7]; this corresponds closely with PS2 monomers found in thylakoids of higher plants, where they occur exclusively in the stroma region[8,9].

Functionally, some of these monomeric particles show high oxygen evolution[6,10–12], confirming that the monomer is the smallest PS2 unit that can split water. We will refer to this basic functional unit as an oxygen-producing PS2 core complex.

**The PS2 dimer.** Oxygen-producing PS2 core complexes were first shown to exist as dimers in a thermophilic cyanobacterium[6]. In electron micrographs, this 'dimer', which has recently been resolved to much higher resolution, has top-view dimensions of 10 · 17 nm[5,13]. By treatment with mild detergent it can be converted easily to particles of a shape and size corresponding to a monomer. Its dimensions, subunit content and stoichiometry,

*The Psb nomenclature refers to the phototrophic purple bacteria photosystem 2.

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shape and molecular mass [about 450–500 kDa as determined by high-performance liquid chromatography (HPLC)-size exclusion[6] and electron microscopy (EM) image analyses[6,13]] confirm that it is composed of two monomeric core complexes.

Dimeric PS2 cores have also been isolated and characterized from higher plants. Image-analysis of negative-stained single particles show a similar size and electron density pattern to that of the oxygen-producing PS2 core dimers isolated from cyanobacteria[5,13]. Contours obtained from the averaged top views of isolated dimeric particles in EM[5] have been used for the model shown in Fig. 2; the two monomeric complexes show a rotational symmetry of towards each other with respect to the centre of the dimer, which is a low electron density area (see below).

Evidence for the existence of PS2 dimers in native membranes also comes from freeze–fracture analyses of thylakoids from both cyanobacteria[7,14] and higher plants (Refs 8, 9), in which the stroma region shows exclusively the monomeric form and the grana region appears highly enriched for the dimer. The observed lateral separation of monomers and dimers is strongly supported by biochemical analysis of maize stroma and grana membranes[15].

This structural information also allows an observation made in 1964 of large tetrameric particles (185 × 155 Å) in thylakoid membranes from higher plants to be re-interpreted. These were postulated to be 'quantasomes' and to act as minimal photosynthetic units[16]; they might well be made up of dimeric PS2 core complexes[15,17]. The tetrameric particles disappear – concomitant with the loss of water-splitting activity – upon removal of the 33 kDa extrinsic protein (PsbO) and two others, the 17 kDa and 23 kDa proteins (PsbQ and PsbP, respectively) that are associated with the oxygen-evolving apparatus. The dimeric structure that is revealed can revert to tetramers on reconstitution of the extrinsic proteins[17]. These structural features are not observed in mutants lacking PS2 (Ref. 18). Also, on the only occasion when PS2 particles isolated from grana thylakoids have been described as monomers[19], their mass, size and shape are consistent with those of PS2 dimers[5,13,20,21].

Although water-splitting activity of PS2 monomers and dimers isolated from the thermophilic cyanobacterium *Synechococcus* is similar[6], recent data obtained with spinach cores indicate that the dimeric state is more stable and functionally active compared to isolated monomers (B. Hankamer *et al.*, unpublished).

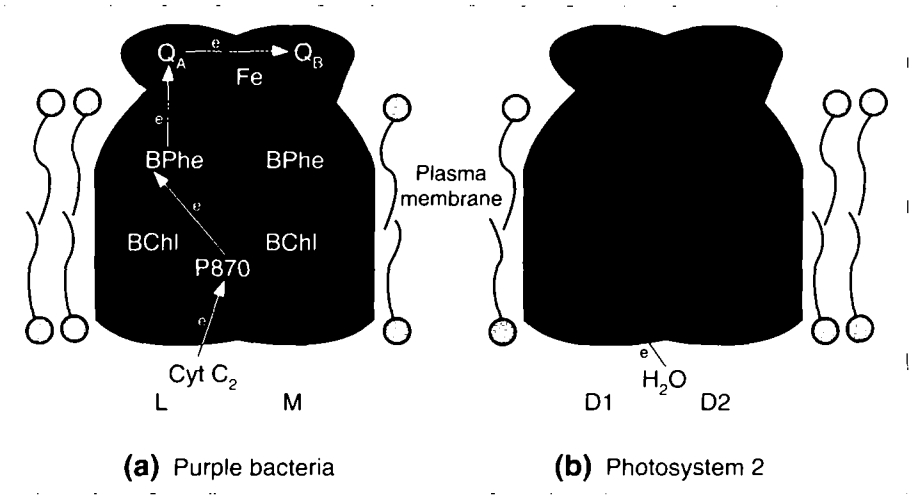


**Figure 1**

Scheme comparing the central electron transport components of **(a)** photosynthetic purple bacteria and **(b)** photosystem 2 (PS2), both of which are quinone-type reaction centres. The related primary electron donors (chlorophyll P680 in PS2 and P870 chlorophyll in purple bacteria), primary electron acceptors (pheophytin, Phe and bacteriopheophytin, BPhe), and quinones, which act as secondary and tertiary electron acceptors ($Q_A$ and $Q_B$), are shown. These redox components are sequentially arranged within two homologous reaction centre proteins, the D1–D2 subunit in PS2 and the L–M subunit in purple bacteria.

## Subunit arrangement in the PS2 core complex

Recent data obtained by negative staining of isolated particles[5] and two-dimensional crystals[15,20,21] of PS2 from both cyanobacteria and higher plants have led to a model of the possible subunit arrangements within the dimeric PS2 complex (Fig. 2).

**The CP43 subunit.** By comparison with electron micrographs of isolated PS2 complexes that lack the CP43 subunit[22], we place CP43 towards the periphery in our model (Fig. 2a); this is in line with the finding that this subunit is the last one to be incorporated during PS2 core assembly, and that the deletion of the *psbC* gene does not prevent the assembly of a PS2 complex *in vivo*[4,23]. Moreover, CP43 can be removed biochemically from isolated PS2 cores to yield a CP47–D1–D2–cyt $b_{559}$

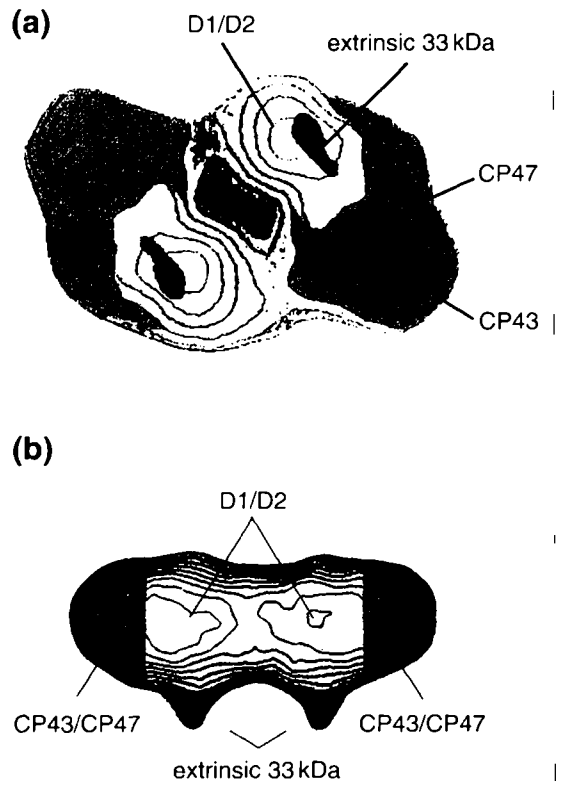


**Figure 2**

**(a)** Top and **(b)** side view of the model for a dimeric photosystem 2 (PS2) complex both in higher plants and cyanobacteria. The model is based on averaged views of electron micrographs with areas showing the largest differences being contoured[5,13]. Colours indicating the suggested positions for PS2 subunits are superimposed on the top and side view[5]. In the top view the position of the extrinsic 33 kDa subunit (PsbO)[5] has been superimposed.

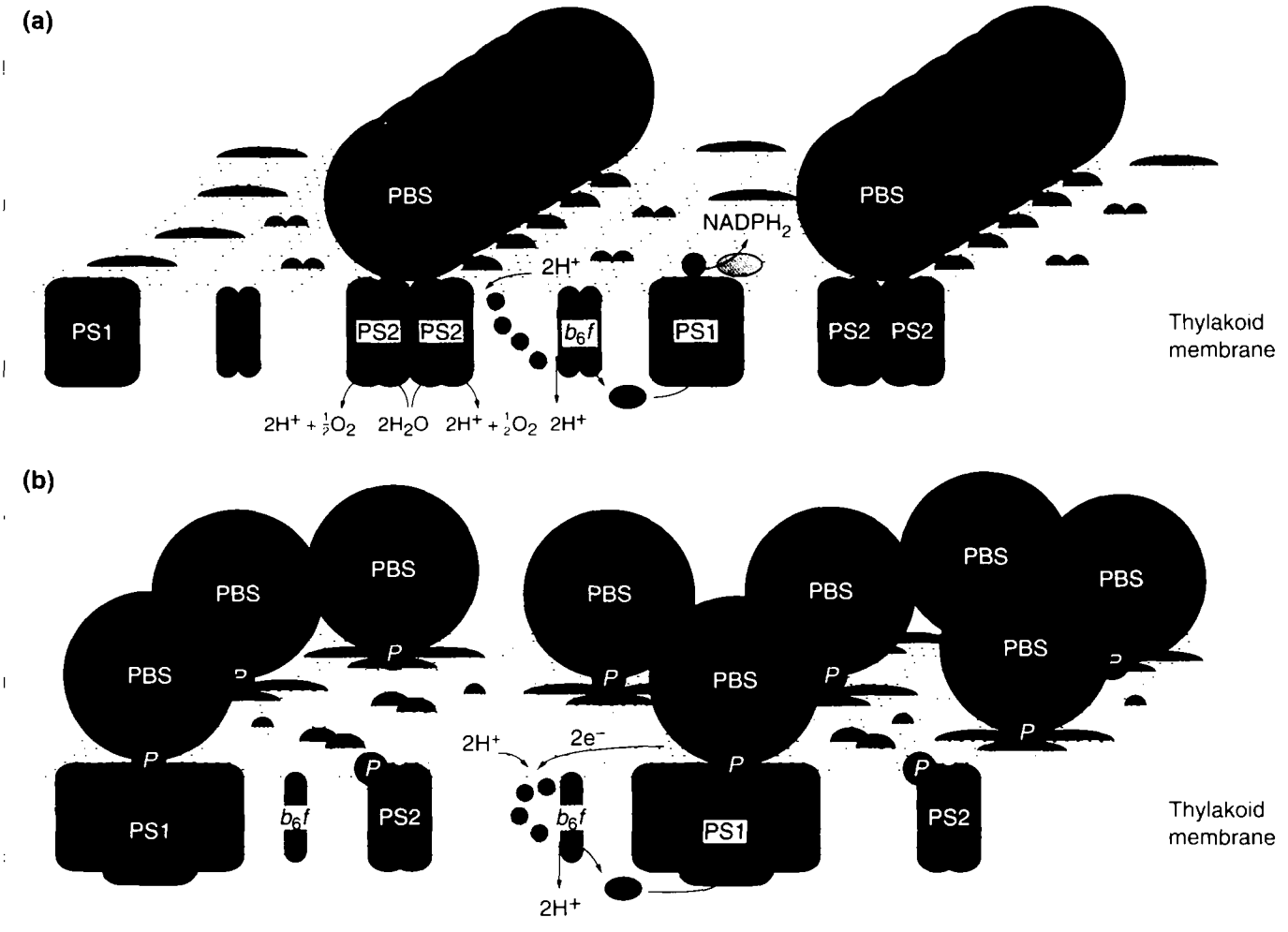


**Figure 3**

Model for state transitions in a cyanobacterial thylakoid membrane (modified from Ref. 29); **(a)** state 1 (favouring linear electron flow, with dimeric PS2, dimeric $b_6f$ and monomeric PS1 complexes) and **(b)** state 2 (favouring cyclic electron flow, with monomeric cyt $b_6f$ and trimeric PS1 complexes; monomeric PS2 is not involved)[27]. Components depicted in the figure are photosystems 1 (PS1) and 2 (PS2) in green, cytochrome $b_6f$ complex (orange), plastoquinone (black circles), plastocyanin (dark blue), ferredoxin (red) and the ferredoxin–NADP oxidoreductase (yellow). The phycobilisome light-harvesting system (PBS) is light blue. For simplicity, other parts of this thylakoid membrane besides the components of the photosynthetic electron transport chain have been omitted. Adapted with permission from Ref. 29

complex[22], and this removal does not induce monomerization of PS2 (Ref. 15).

**The extrinsic 33 kDa subunit (PsbO).** This subunit (depicted in red in Fig. 2) can also be located through comparison of core complexes with and without this subunit[8]. Negative-staining EM data from both cyanobacteria and higher plants suggest that this subunit protrudes out of the membrane plane by about 3 nm[5,11,13], while freeze-etching data show that these structures are exposed at the inner surface of the thylakoid photosynthetic membrane, disappearing concomitantly with treatments that inhibit oxygen evolution[17,22,24]. Furthermore, these results suggest that most of the hydrophilic surface area of PS2 is exposed to the thylakoid lumen and that there is limited protrusion of PS2 proteins on the stromal side[15].

**The CP47 and the D1–D2 subunit.** As the extrinsic 33 kDa subunit is shielding the water-splitting manganese complex, which in turn is close to P680, the yellow area around the 33 kDa subunit (Fig. 2) can be assumed to be occupied by D1–D2, leaving CP47 in the space between D1–D2 and CP43. Alternatively, it cannot be ruled out that the positions of CP47 and D1–D2 can be switched, resulting in a separation of CP43 and CP47 by D1–D2. Both arrangements are in agreement with biochemical analysis, suggesting that CP47 might play a role in maintaining the dimeric structure[15] with antiparallel arrangement of the two monomers.

Interestingly, several other membrane protein complexes have also been reported to be dimeric (for review, see Ref. 24). Among them is the cyt $b_6f$ complex of the thylakoid membrane, the cyt $bc_1$ complex and the cytochrome oxidase of the mitochondrial membrane, the anion carrier of erythrocytes, rhodopsin, the ($Na^+$, $K^+$) ATPase and the ADP/ATP carrier protein. In the case of the cytochrome oxidase, the proton pumping apparently requires a dimeric structure, while the monomeric complex can only catalyse cyt *c* oxidation. The cyt $bc_1$ complex appears to be equally active in both monomeric and dimeric forms, while the cyt $b_6f$ complex has been reported to be considerably less active in its monomeric form[25].

## Physiological relevance of monomeric/dimeric structure

**Cyanobacteria.** The model outlined in Fig. 2 indicates that the antenna chlorophyll-binding subunits CP43 and CP47 sequentially channel excitation energy

to the D1–D2 heterodimer of the reaction centre. In addition it seems possible that energy can be distributed between the two reaction centres of the dimer via the CP47 subunits; this could be important for ensuring optimal usage of excitation energy[26]. Fluorescence induction measurements support this idea: monomeric complexes show an exponential increase of fluorescence intensity with time, while dimers show a sigmoidal increase in fluorescence intensity and a positive connectivity[26,27]. This finding is consistent with the idea of cooperativity existing between the two connected monomers[28].

In cyanobacteria, PS2 complexes also serve as binding sites for an additional hydrophilic light-harvesting system, the phycobilisome (PBS). Freeze-fracture electron micrographs show rows of hemi-discoidal PBSs on the surface of cyanobacterial thylakoid membranes, with a periodicity that matches that of dimeric PS2 particles in the membrane underneath. This finding suggests that the PBS–PS2 supercomplexes are composed of two PS2 complexes and one PBS[7]; an arrangement that is also confirmed by biochemical analyses and energy transfer studies[29]. Also, the two basal PBS core cylinders that are responsible for the PBS–PS2 connection have a compatible size to the oxygen-evolving PS2 core dimer[7]. The organization of the PBS–PS2 supercomplexes into tightly arranged rows not only allows for a high packing density of PBSs, but also potentially for high-efficiency excitation-energy transfer between adjacent PS2 units. This would result in an energy-conducting fibre system that facilitates an efficient energy distribution along the plane of the thylakoid[7], and thus help to optimize light harvesting.

However, the association of PBS and the dimerization of PS2 seems to be dynamic, as more-or-less randomly distributed PBSs have also been observed on the surface of cyanobacterial thylakoid membranes; the extent to which PBSs are organized into rows seems to be related to the light condition during growth[29]. Uncoupling or partial dissociation of PS2 and PBS apparently results in their lateral redistribution, which in turn alters the energy distribution among the photosystems. By these so-called 'state transitions' cyanobacteria respond to preferential excitation of PS2 or PS1 by selective enhancement of excitation energy transfer to the less active photosystem.

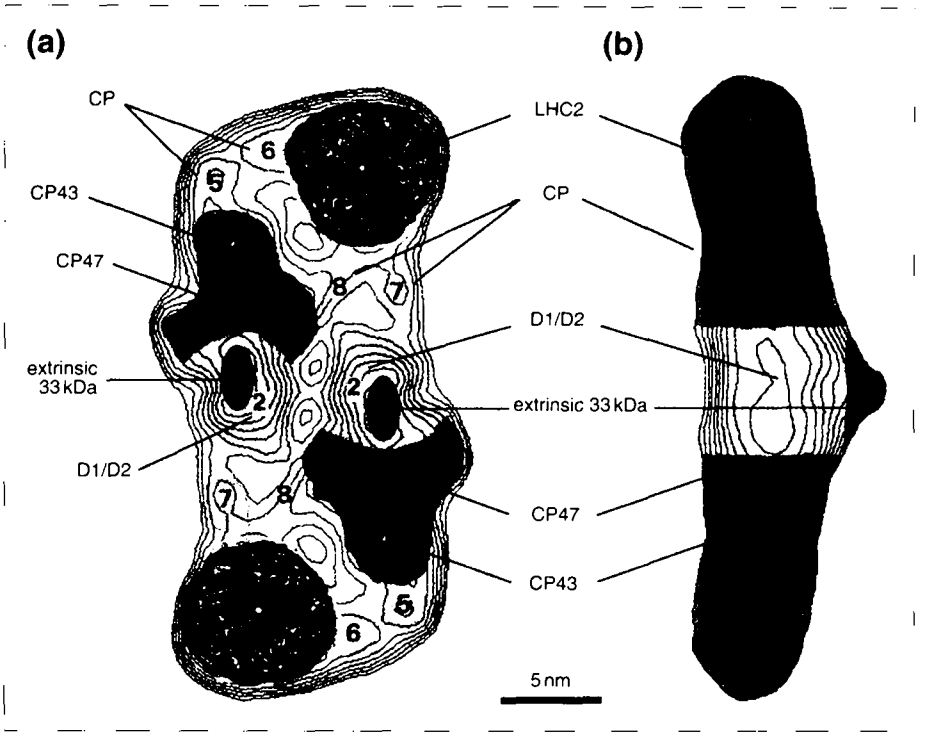


**Figure 4**

**(a)** Top view and **(b)** side view of the model for a dimeric light-harvesting complex 2 (LHC2)–photosystem 2 (PS2) complex in higher plants. The model is based on averaged views of electron micrographs with areas showing the largest differences being contoured[5]. As for Fig. 2, colours indicate suggested positions for subunits. So that this figure can be compared directly with Fig. 2, the hydrophilic 18 kDa and 23 kDa subunits, which are usually associated with the extrinsic 33 kDa subunit of higher plants, were removed before structural investigations on this complex. Yellow and red areas indicate corresponding central domains in cyanobacteria and chloroplasts. CP might represent the chlorophyll-binding proteins CP29, CP26 and CP24.

A model has recently been proposed that tries to combine structural and physiological data[27]. Figure 3 illustrates the most important features of this model. Under light conditions that favour the photochemistry of PS1 – so called 'state 1' – PBSs are attached to dimeric PS2, while under conditions when light preferentially excites PS2 ('state 2') PBSs become functionally connected to trimeric PS1. The redistribution of PBSs might be caused by the dissociation of dimeric PS2 into monomers and a concomitant trimerization of the PS1 complex. Alternatively, in state 2, PBSs might still be connected to one monomer of the previous PS2 dimer, while trimeric PS1 replaces the other PS2 monomer to form a close association with PS2.

Direct energy transfer from PBSs to PS1 under 'state 2' has been shown by spectroscopic measurements of cyanobacterial thylakoid membranes[29], and the maximal quantum efficiency of this transfer is enhanced considerably in mutants that lack PS2, suggesting a specific PBS–PS1 complex[30]. As the cyt $b_6f$ complex has also been reported to exist in both highly active dimeric and low-active monomeric forms, the above discussion could herald a general principle of energy distribution within the thylakoid membrane as a result of a dynamic equilibrium of mono- and oligomeric forms of all three membrane protein complexes of the photosynthetic electron transport chain, i.e. PS1, PS2 and the cyt $b_6f$ complex[27]. A dynamic clustering of photosystems caused by different light regimes was also reported for rhodophyta and reflects changes in functional domains that result in enhancement of the quantum yield owing to maximized cooperativity between the photosystems[31].

**Higher plants.** By contrast, green algae and higher plants have their thylakoid membranes structurally organized into stacked grana and unstacked stroma regions, with the stroma membranes containing most of the PS1 and the grana regions highly enriched in PS2. The cyt $b_6f$ complex is more or less evenly distributed among both membrane regions.

Furthermore, PS2s of green algae and higher plants do not possess PBSs, but

instead have intramembranous antenna protein complexes that bind both chlorophyll *a* and chlorophyll *b* for additional light harvesting. These proteins are predominantly CP29 (Lhcb4), CP26 (Lhcb5), CP24 (Lhcb6) and the light-harvesting complex 2 (LHC2 or Lhcb1–Lhcb2). Biochemical and structural studies have shown that they are closely associated with PS2, but the level of association differs between grana- and stroma-located PS2 complexes: stromal PS2 complexes occur exclusively in the monomeric form and have few chlorophyll *a*- and chlorophyll *b*-binding proteins associated with them (for summary, see Refs 28, 32), while a close association of the various light-harvesting complexes with the oxygen producing dimeric PS2 cores, occurring exclusively in the grana, has been suggested[8,9,32]. Biochemical fractionation by gel electrophoresis failed to reveal any association of LHC2 with monomeric PS2, and was only seen with dimeric PS2 (Ref. 33). Obviously, the conversion between monomeric and dimeric forms of PS2 modulates its function and plays a role in the degradation–repair cycle associated with D1 turnover[34], which in turn might involve reversible phosphorylation[35]. In more detail, EM studies of wild-type PS2 and mutants that lack chlorophyll *b* and all chlorophyll *a*- and chlorophyll *b*-binding proteins[9,18] suggest that the small chlorophyll-binding proteins CP29, CP26 and CP24 connect the dimeric core complex to the trimeric LHC2 (Refs 5, 9, 18, 36); this has resulted in the model presented in Fig. 4.

A comparison with Fig. 2a clearly shows the dimeric core complex in the central domain. If the side view of this model is compared with that presented in Fig. 2, it can be seen that the two extrinsic 33 kDa subunits are overlapping and therefore appear as a single (red) subunit with a maximal height of 9 nm in the central area. Figure 4 also indicates (by comparison with Fig. 2) the likely position of the various chlorophyll *a*/*b*-containing LHC subunits on either side of the dimeric core. By contrast to most other models of the PS2 antenna complex (summarized in Ref. 32), which are based on biochemical data and cannot indicate the precise position of the antennae, the structure given in Fig. 4 suggests a perfect rotational symmetry of the dimeric state, including all antenna systems. The assignment of protein densities with specific chlorophyll *a*- and chlorophyll *b*-binding proteins in Fig. 4 is consistent with several pieces of biochemical data (for review, see Ref. 32) and especially prominent for the trimeric LHC2 (Ref. 36).

Functionally, the monomeric proteins CP29, CP26 and CP24 have a relatively small contribution to the PS2 antenna system, as together they bind only 15% of the PS2 chlorophyll. However, the inner localization of this antenna system is consistent with its proposed role in regulating the efficiency of excitation energy transfer from the 'outer antenna', LHC2, to the core[32]. By contrast, the trimeric LHC2 complexes (Lhcb1–Lhcb2) contain about 63% of the PS2 chlorophyll and, therefore, represent the major antenna system for PS2.

The light-harvesting antenna of the dimeric PS2 of the grana region was suggested to consist of one copy each of CP29, CP26 and CP24, and two to four trimers of LHC2, resulting in an antenna size of 230–250 chlorophyll molecules per reaction centre[32]. As the antenna size of the LHC2–PS2 complex in Fig. 4 was determined to contain only about 100 chlorophyll molecules, this difference could be accounted for by a ratio of two or three additional trimeric LHC2s per reaction centre. These additional LHCs might be responsible for forming contacts between the dimeric LHC2–PS2 complexes in the membrane, thus, building an antenna network that spreads across the whole grana region. Indeed, two distinct subpopulations of LHC2 with slight differences have been shown to exist[37]. Therefore, it is possible that these subpopulations of LHC2 could be flexible under different light conditions and might migrate – depending on their degrees of protein phosphorylation – to the stroma-exposed thylakoid regions to associate with PS1. This arrangement is comparable to the PBSs in cyanobacteria and red algae.

The equidistant arrangement of PS2 in grana as seen in freeze-fracture sections indicates that PS2, surrounded by their antenna systems, form random networks[24]. The idea of a network of pigment proteins covering the membrane is supported by the high protein density of the grana membrane, implying the possibility of an efficient excitation energy transfer over long distances. This suggestion is supported by fluorescence induction measurements with thylakoids of higher plants giving data that are consistent with energy transfer between PS2 dimers in the grana region[38].

In summary, it seems that the dimerization of PS2 core complexes in higher plants, as well as in cyanobacteria, is an important organizational and functional state, playing a key role in the interaction with secondary antenna systems, i.e. PBSs and chlorophyll *a*/*b*-binding proteins, respectively.

### Evolutionary significance

Cyanobacteria might serve as a model system for higher plants in an evolutionary sense. In cyanobacteria, PS2s are clustered in rows of PS2 dimers, to which PBSs are attached. In higher plants, a very similar dimeric organization of PS2 is seen in the grana regions, which would allow efficient photosynthesis. By analogy to the cyanobacterial PBSs, higher plants exhibit several (between six and eight) trimeric LHC2 complexes associated to varying degrees with a dimeric core complex. Therefore, a kind of PS2 network is created in both cases.

In higher plants, this PS2 network gives rise to grana[24], while the stroma regions contain only monomeric PS2 (Ref. 15). By contrast, the cyanobacterial thylakoid membrane not only contains all components of photosynthetic electron-transfer machinery, but also the respiratory electron-transfer chain. These interconnected PS2s in cyanobacterial thylakoid membranes under 'state 1' conditions might be regarded as a precursor of the specialized 'grana networks' of higher plants, while the cyanobacterial 'state 2' [i.e. PBSs attached to PS1 (Ref. 29)] might be the precursor of the stroma region. In both cases, the clustering of dimeric PS2 also results in an effective separation from PS1, which is necessary according to the significant difference in the kinetics of their trapping reactions (PS2 is slow compared with PS1)[39]. A clear evolutionary link between organisms containing PBSs and chlorophyll *b*-based LHCs is further indicated by the coexistence of both types of antenna system in several rhodophytes[40] and the recent finding of domains with highly enriched PS1 or PS2 in thylakoid membranes of cyanobacteria[41].

It appears that a dimeric complex is preferred for the basic water-splitting function of PS2, irrespective of being prokaryotic or eukaryotic. As bacterial reaction centres are not arranged as dimers and they do not split water and evolve oxygen, the dimeric arrangement in PS2 might have emerged

with the transition to an oxygenic atmosphere, and thus, might be vital to optimize and sustain the water-splitting function[21].

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